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The Strawberry Bank Lagerstätte reveals insights into Early Jurassic life

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Abstract: The Strawberry Bank Lagerstätte provides a rich insight into Early Jurassic marine vertebrate life, revealing exquisite anatomical detail of marine reptiles and large pachycormid fishes thanks to exceptional preservation, and especially the uncrushed, three-dimensional nature of the fossils. The site documents a fauna of Early Jurassic nektonic marine animals (five species of fishes, one species of marine crocodilian, two species of ichthyosaurs, cephalopods, and crustaceans), but also over 20 species of insects. Unlike other fossil sites of similar age, the three-dimensional preservation at Strawberry Bank provides unique evidence on palatal and braincase structures in the fishes and reptiles. The age of the site is important, documenting a marine ecosystem during recovery from the end-Triassic mass extinction, but also exactly coincident with the height of the Toarcian Oceanic Anoxic Event, a further time of turmoil in evolution.

21 **A long-forgotten site in Somerset, UK**

22 The early Toarcian Strawberry Bank Lagerstätte from Ilminster, Somerset, UK, has produced
23 a substantial assemblage of fossils of marine nektonic animals, including ichthyosaurs,
24 crocodiles, fishes, cephalopods, and crustaceans, together with abundant remains of insects
25 from the nearby land. These fossils preserve soft parts in certain cases, but they are
26 remarkable for the fact that many are preserved in three dimensions, allowing unique access
27 to anatomical details otherwise unknown from other Early Jurassic faunas, including such
28 coeval Lagerstätten as Holzmaden in Germany. What is especially extraordinary is that the
29 site was found in the 1840s and yielded thousands of exquisite specimens, and yet has
30 remained largely unknown since then.

31 In the late 1840s, Charles Moore (1815-1881), a locally born geologist, discovered a
32 diverse and spectacularly preserved marine fauna within limestone nodules from a small
33 quarry on Strawberry Bank. He recognised its age as Upper Lias, and within the *falciferum*
34 Ammonite Zone of the Toarcian. Moore made an extensive collection from the horizon, and
35 noted the Strawberry Bank fossils in several papers (Moore 1853, 1866), but never described
36 the fauna in any detail. The fishes were reviewed by Woodward (1897), and brief mentions
37 were made in wider reviews by Rayner (1948) and Patterson (1975), with further references
38 to the fishes and reptiles by McGowan (1978) and Duffin (1979). Otherwise, the Moore
39 collection was neglected (Duffin 1978; Copp *et al.* 1999), and it was not afforded the
40 attention it deserved.

41 The Strawberry Bank site is unusual in that the specimens were collected by one person
42 during a limited span of time. Nearly all of these are held by Bath Royal Literary and
43 Scientific Institution (BRLSI) and the South West Heritage Trust, Taunton (TTNCM), with
44 one or two specimens, presumably exchanged, in the Natural History Museum, London, and
45 the National Museum of Ireland, Dublin. The Bath and Taunton collections have been

recurated and concerted studies began after 2005. The first publication was a paper describing the crocodilian *Pelagosaurus* (Pierce and Benton 2006), and one of the three-dimensional skulls was CT-scanned, with excellent results (http://digimorph.org/specimens/Pelagosaurus_typus/whole/). Further work included a revision of the ichthyosaur specimens (Caine and Benton 2011). The aim of this paper is to introduce the geology and stratigraphy of the Strawberry Bank Lagerstätte, to review its remarkable fossils, and to explore their mode of preservation and significance.

Location and age

The Strawberry Bank site is located within the town of Ilminster, Somerset, UK, in the middle of the snaking outcrop of Lower Jurassic that runs from Dorset to Yorkshire (Fig. 1a). These Lower Jurassic Lias Group sediments were laid down in the European epicontinental sea at the north-western margin of the Tethys Ocean (Simms *et al.* 2004; Golonka 2007). The stratigraphic sequence (Fig. 1b) is divided into the Marlstone Member and Barrington Member ('Beds') of the Beacon Limestone Formation.

Moore (1866) indicated that the quarry was situated on the southern slope of Beacon Hill, and Duffin (1979) located it as north of the High Street in Ilminster, in an area called the Triangle (National Grid Reference ST 361148). This area is filled and built over, so there is no chance to see the successions from which Moore made his collections. However, there may be hope in the future of locating lateral exposures of the fossiliferous horizons.

The vertebrate fossils at Strawberry Bank are contained within calcareous concretions that preserve them in three dimensions (see Box 1). These concretions occur within a unit traditionally called the 'Junction Bed', 6 m thick at Ilminster and 0.7–2.0 m thick around Bristol. This unit, understood in the broad sense, was formalised as the Beacon Limestone Formation by Cox *et al.* (1999), overlying the Dyrham Formation, and lying below the

Bridport Sand Formation, in the Wessex Basin, including the Dorset coast and South Somerset. In the Ilminster area, the succession is expanded, and the Beacon Limestone Formation comprises the Marlstone Member overlain by the Barrington Member (Bristow and Westhead 1993; Cox *et al.* 1999).

Moore (1866) provided a detailed measured section for the Upper Lias at Strawberry Bank, the only such section by an eyewitness before the quarry was closed (Fig. 1c). However, in the 1920s, excavations were made at Barrington Court, 5 km northeast of Ilminster, and Hamlet (1922) matched his beds 3, 4, and 7 with Moore's section. The Moore section spans Hamlet beds Middle Lias 1–2 and Upper Lias 1–12. Cope *et al.* (1980) equate Hamlet's Upper Lias beds 3–11, totalling 1.45 m in thickness and including the *Leptaena* Bed and the Fish Bed, with the *Harpoceras exaratum* Ammonite Subzone of the *Harpoceras falciferum* Ammonite Zone. The 'saurian and fish bed' (Hamlet's Upper Lias Bed 4) then lies low in the *exaratum* Ammonite Subzone. When using continental Jurassic zoning schemes, Moore's 'Leptaena Clay' and 'Fish Bed' are assigned to the Lower Toarcian Serpentinum Chronozone and Elegantulum Subchronozone, equivalent to the foraminiferal zone FJ9 (Boomer *et al.* 2009).

The exact age is determined from a high-resolution U-Pb radio-isotopic age of a sample from the initial reversed polarity phase (Pl-To R) of the Karoo basalts in South Africa, with a corrected age of 182.7 ± 0.7 Ma (Gradstein *et al.* 2012), corresponding to the basal *tenuicostatum* Ammonite Zone (Fig. 1b). Durations of the ammonite zones in the Toarcian are based on cycle-stratigraphy of zones in France and Portugal, so giving an age of c. 183 Ma for the *falciferum* Ammonite Zone. This is confirmed by correlation of ash beds in a sedimentary succession with ammonites in Peru, and by matching carbon isotopic excursions between continents (Sell *et al.* 2014). High-precision U-Pb dating of zircons from the Peruvian ash beds place the top of the *tenuicostatum* Zone at 183.22 ± 0.25 Ma, and the

middle of the *bifrons* Zone at 181.99 ± 0.13 Ma, so confirming an age for the intervening *falciferum* Zone around 183 Ma.

A time of environmental crisis

The *falciferum* Zone corresponds in age precisely to the height of the Toarcian oceanic anoxic event (T-OAE). The T-OAE spanned the upper part of the underlying *semicelatum* Ammonite Subzone, and extended through the *exaratum* Ammonite Subzone, peaking at about one-third of the way through the latter (Schootbrugge *et al.* 2005). The entire T-OAE isotopic excursion has been estimated as lasting 0.3–0.5 Myr (Boulila *et al.* 2014) or 0.6 ± 0.1 Myr (Huang and Hesselbo 2014), with the two major anoxic episodes, termed T-OAE1 and T-OAE2 falling on either side of the 183 Ma age estimate (Ikeda and Hori 2014; Sell *et al.*, 2014). The substantial carbon isotopic anomaly has been explained by input of large volumes of isotopically light carbon from the Karoo-Ferrar basaltic province (Suan *et al.* 2010; Burgess *et al.* 2015).

The T-OAE was a time of environmental turmoil and extinction. Suan *et al.* (2010) identified a cooling episode immediately before the T-OAE, when sea surface temperatures fell by ~ 5 °C, followed by prolonged warming of ~ 7 – 10 °C through the early Toarcian. The greenhouse warming and biocalcification crisis were associated with volcanic eruption, possible methane release and sea level changes associated with icecap development and melting (Kemp *et al.* 2005; Wignall *et al.* 2005; Suan *et al.* 2010; Caruthers *et al.* 2013).

The T-OAE extinction extended through five ammonite zones, spanning 4 Myr, and peaking in the *falciferum* Zone, at 183 Ma (Little & Benton 1995; Danise *et al.* 2015). The significance of the Strawberry Bank Lagerstätte is that it dates to immediately after these assembled crises, within the first 1 Myr of recovery time, when oceans were still experiencing the peak of the negative carbon isotopic shift, and following the peak of

extinction, but while extinction rates were still high. The extinction among nekton, the bulk of the Strawberry Bank fauna, was controlled by variations in weathering, nutrient runoff, and primary productivity (Danise *et al.* 2015).

Faunal Overview

Invertebrates

By far the most impressive invertebrates from Strawberry Bank are the insects, representing many typical orders of the Early Jurassic, confirming that land was nearby (see Box 2). The high number of complete beetles with their elytra closed indicates that they were washed into the area of deposition, which was probably very close to a land mass.

Among marine invertebrates are rare crustaceans, some of which belong to the extinct group Thylacocephala, the first such records from the Mesozoic of the UK. Thylacocephalans are of uncertain affinities, usually classed as crustaceans, and allied variously with barnacles, crabs, remipedes, or branchiopods. Other crustacean remains appear to be barnacle plates and at least one species of large decapod crustacean, *Coleia moorei*.

Ammonites, brachiopods, bivalves, and other typical marine fossils have been reported from below and above the nodule-bearing bed, but they are relatively rare in and around the nodules. Several specimens of teuthid cephalopods occur, preserving their ink sacs. All these invertebrates await detailed study.

Fishes

There are at least five actinopterygian taxa, including two small bony fishes. The leptolepiform *Leptolepis* (Fig. 2b) and the semionotiform *Lepidotus* are 4–8 cm and 40–45 cm long, respectively. In both cases, the body is fusiform, the paired fins are small, the dorsal

and anal fins are short and deep, and the caudal fin is short and more-or-less symmetrical. The head is heavily ossified, and the strong, short jaws are lined with compressed marginal teeth and stouter inner teeth. The scales are thick and shiny-surfaced, rhombic in shape. The amiiform *Caturus* is known two specimens, including an isolated neurocranium (BRLSI M1288), which Rayner (1948) described in detail from serial sections.

Most important is the pachycormiform *Pachycormus* (Fig. 2a, c-e), with total lengths ranging from 23.5cm (BRLSI M1337) to 85 cm (BRLSI M1308). Most parts of the anatomy have been preserved in exquisite detail. Pachycormiforms were nearly all large, and they are characterised by having reduced pelvic fins and a bony rostrum. There are 17 genera in Pachycormidae, ranging in age from Early Jurassic to Late Cretaceous. Their relationships are debated, although they are generally placed close to semionotiforms, aspidorhynchids, and pholidophorids, on the teleost stem (Friedman *et al.* 2010; Friedman 2011; Arratia 2013).

The Ilminster pachycormid specimens can nearly all be assigned to the type species, *Pachycormus macropterus* (Blainville 1818), described originally from the Toarcian of Grandmont, Beaune in France, and later also from the Toarcian of southern Germany. One Ilminster specimen, BRLSI M1308, is larger than the others (estimated length, 85 cm), and might belong to the closely related *Saurostomus esocinus* Agassiz, 1833, as suggested by Woodward (1897). The Ilminster *Pachycormus* has a strongly constructed head (Fig. 2a). The eye is large and equipped with an ossified sclerotic ring. The teeth are small, stout, and pointed. The pectoral fins (Fig. 2e) are elongate and scythe-like in shape, with rays that bifurcate posteriorly, giving the back edge of the fin a frayed appearance, typical of the clade. The tail fin is symmetrical, with long, symmetrical lower and upper portions; taken together, the depth of the tail fin is nearly half the length of the body, a remarkably large tail fin, as seen also in other pachycormiforms, and presumably evidence of powerful, fast swimming.

Reptiles

Ichthyosauria. Strawberry Bank has yielded eight ichthyosaur skeletons preserved in three dimensions, some with soft tissues (Fig. 3a-c). These ichthyosaurs were first noted by Moore (1866), and he named them all *Ichthyosaurus acutirostris*, but they were subsequently reidentified by McGowan (1978) as *Stenopterygius hauffianus*. Caine & Benton (2011) recognised two distinct taxa, *Stenopterygius triscissus* and *Hauffiopteryx typicus*. Further work on 3D scans (Marek *et al.* 2015) shows details of the palate and braincase in *H. typicus*, and suggests that this species might instead belong to the genus *Leptonectes*.

Most striking is that the specimens are all juveniles (five specimens) or infants (three specimens), ranging from one-tenth to one-half the normal adult length of the species. The small size of the ichthyosaurs and crocodilians, and their possible juvenility, might indicate that the Strawberry Bank deposit was formed in a shallow-water, protected area that acted as a seasonal nursery for some of the marine reptiles.

The diet of the ichthyosaurs consisted of small fishes, belemnites and squid-like cephalopods (Motani 2005). The two Ilminster ichthyosaurs, interestingly, appear to show different dietary adaptations: *Hauffiopteryx typicus* has small, slender, pointed teeth, suggesting the ‘pierce guild’ of Massare (1987), marine reptiles that snatched fast-moving fish and impaled them on sharp teeth to prevent their wriggling free. On the other hand, *Stenopterygius triscissus* has larger, more curved teeth, indicating the ‘smash guild’, ichthyosaurs that grasped and punctured hard-shelled prey such as cephalopods.

Mesoeucrocodylia. Moore (1853) reported three well-preserved individuals of *Teleosaurus*, later (Moore 1866, 1870) assigned to the species *Teleosaurus temporalis*. They were then identified as two species, *Pelagosaurus moorei*, and *Pelagosaurus typus* (Moore 1879; Wilson 1893; Woodward 1893). Duffin (1979) presented a description of the skull of the

juvenile, and assigned the Ilminster material to *P. typus*, a view followed by Pierce and Benton (2006) in their full description. The material comprises four isolated skulls and associated postcranial skeletal elements, as well as two articulated specimens, one of which (BRLSI M1418) is a small juvenile (Fig. 3d, e).

The skull of the Ilminster *Pelagosaurus typus* is narrow, long, and heavily sculptured (Fig. 3d). The snout comprises more than 75% of the total skull length. It is narrow anteriorly, with teeth that are well spaced, needle-like and recurved. The posterior portion of the skull is broad, and the orbits circular and facing upwards. The limbs are reduced, suggesting that *Pelagosaurus* may have had limited mobility on land. The legs and feet are larger, and presumably used in swimming and steering. The torso bears a broad abdominal armour below, and a double series of broad armour plates from the back of the head to the tip of the tail. The tail is long and slightly deepened and laterally flattened, confirming its likely use as a propulsive organ that beat from side to side.

The Ilminster *Pelagosaurus* appear to have been active, lightweight swimmers, classified as high-speed pursuit predators (Massare 1988). *Pelagosaurus* preyed on small fishes such as *Leptolepis*, as well as perhaps crustaceans and soft-bodied animals, as well as possibly even insects flying over the surface. The juvenile *Pelagosaurus* (BRLSI M1418) even contains a vertebral column and caudal fin of *Leptolepis* within its rib cage, possible primary evidence of diet (Pierce and Benton 2006).

Taphonomy

Overall, the Strawberry Bank fauna presents detailed evidence of life in near-shore, shallow waters (Fig. 4). The taphonomy cannot be studied *in situ*, and details must be gleaned from specimens and historical accounts (Duffin 1978, 1979). The fishes, reptiles, ammonites, belemnites, and teuthoids are generally preserved in carbonate-rich concretions. They are

usually completely enclosed, and sometimes the concretion mimics the rough shape of the fossil; this is especially the case for the fishes. With larger specimens, for example some of the ichthyosaurs and crocodiles, parts of the skeleton may be surrounded by a concretion, and other portions may stick out beyond the concretion. The insects, crustaceans, and *Leptolepis* are preserved as isolated specimens in muddy limestone, with no sign of concretions, though it is not clear whether Moore trimmed the blocks down from a larger concretion in some of these specimens, as the matrix is lithologically similar.

The fish and reptile skeletons are generally articulated, with varying degrees of disarticulation of the skull and girdles. These probably became detached following microbial scavenging and storm activity, which might also explain the absence of other skeletal elements, particularly the tail, snout tip, and distal paddle elements (cf. Martill 1987, 1993). The bones show a range of preservation quality, from immaculate, with striations and capillary canals, to poorly preserved eroded surfaces. In the fish specimens, the scales, branchiostegal bones (Fig. 5a), and fin rays are in pristine condition, with surface texture and lustre still preserved. Evidence from thin sections suggests that branchial arches, branchial rays, and gill rakers may commonly be preserved internal to the fish skulls. Gut traces are phosphatised in at least three fish specimens (Fig. 5b). Soft tissue is present in the ichthyosaurs (Fig. 5c, d) as both a white layer (probably calcium phosphate) with structure and a greyish amorphous material. Teuthoid cephalopods may show soft tissues such as the ink sac, stomach, gladius, and possibly mantle/fin structures (Fig. 5e).

The high degree of articulation of the fish and reptile skeletons suggests that: (1) post-mortem drifting was minimal and individuals died where they lived; (2) carcasses reached the sea floor soon after death, prior to the onset of decay; (3) once on the sea floor, nodule formation began very rapidly and the carcasses were rapidly buried in sediment and/or sank completely into the soupy bottom muds; and (4) after initial burial, the sea bed conditions

represented a low-energy setting. These observations suggest that the Strawberry Bank deposit is an *in situ* accumulation (Konservat Lagerstätte) rather than a site of concentration of skeletons from a wider area (Konzentrat Lagerstätte).

Burial was probably fast, as suggested by the absence of encrusters and burrowers on the bone surfaces (Martill 1987, 1993). In addition, the pristine condition of the scales and tail spines of the fish specimens also indicates rapid burial. The carbonate concretions provided protection against compression from overburden pressures during diagenesis and thus preserved the fossils in three dimensions. The modes of preservation require further study (Box 1).

Comparisons

In assessing the significance of the Strawberry Bank Lagerstätte it is essential to consider coeval deposits offering similar preservation. Closest in these regards are two sites in France. Woodward (1908) reported a three-dimensional *Pachycormus* from the ‘Upper Lias of La Caine (Calvados)’. The paper provides no further geological information, but the specimen presumably came from the ‘Argiles à Poissons’ of La Caîne in Normandy, source also of specimens of the ichthyosaur *Stenopterygius longifrons*, a juvenile ichthyosaur, and the crocodilian *Pelagosaurus* (Dugué *et al.* 1998). The Argiles à Poissons is correlated with the *Harpoceras serpentinus* Zone (= *falciferum* Zone, lower Toarcian), exactly the same age as the Reptile Bed at Strawberry Bank (Dugué *et al.* 1998).

The second French unit, the ‘Couches de Belmont’ in the Lafarge Quarry at Charnay, Beaujolais (Rhône, SE France), is a fossiliferous succession of mudstones, marlstones and limestones of Toarcian to Bajocian age (Suan *et al.* 2013). In horizons dated to the *serpentinum* Zone (= *falciferum* Zone), two ichthyosaurs were preserved in three dimensions, showing uncrushed bones and possible soft tissues, one in bedded limestone and the other in

a calcareous nodule. These fossils add to previous discoveries throughout the Toarcian and Aalenian here, of bony fishes, sharks, ichthyosaurs, plesiosaurs, and marine crocodilians, but these were mainly isolated bones, teeth, and scales (Vincent *et al.* 2013), apart from one nearly complete skeleton, *Temnodontosaurus azerguensis*, from a compressed mudstone of the *bifrons* Zone (Martin *et al.* 2012). At present, the coeval French faunas appear similar to that from Strawberry Bank, but remains are much more sparse.

More famous, and better documented, comparable early Toarcian sites occur at Whitby in Yorkshire and Holzmaden in southern Germany. The vertebrate faunas show major differences in taxa and proportions (Fig. 6, top). Strawberry Bank is dominated by *Leptolepis* and pachycormid fishes, whereas ichthyosaurs are much more abundant at Holzmaden and Whitby, and the latter two sites also yield plesiosaurs and pterosaurs, not known at Strawberry Bank. The entomofaunas of these locations show similar lists of taxa, but proportions are different (Fig. 6, bottom), with dominance by beetles at Strawberry Bank, and by Odonata and Hemiptera at Holzmaden, and Hemiptera and Diptera at Grimmen in Germany.

The Yorkshire sites, focused around Whitby, have yielded numerous specimens of marine reptiles from the lower Toarcian, with 14 specimens from the Jet Rock Formation and 144 from the Alum Shales Formation (*falciferum*, *bifrons* zones; Benton and Taylor 1984). Most of the Yorkshire early Toarcian marine reptiles are different taxa from those at Strawberry Bank, except the small thalattosuchian crocodilian *Pelagosaurus*. The Yorkshire specimens are found in organic mudstones, with individual elements preserved in three dimensions, but bones may be crushed and disarticulated by scavenging and sedimentary processes, and soft tissues are not present.

The early Toarcian marine faunas of the Posidonienschiefer of SW Germany (e.g. Holzmaden, Ohmden, Boll, Banz, Altdorf) are equally well known. The fishes and marine

reptiles come from bituminous laminated shales and grey marlstones, dated to the *tenuicostatum* to *bifrons* Zones of the lower Toarcian. Hauff (1921) records about 350 specimens of ichthyosaurs, about 70 specimens of crocodiles, ten specimens of plesiosaurs, as well as rare pterosaurs, and perhaps 300 fishes, including sharks, and the bony fishes *Lepidotes*, *Caturus*, *Dapedium*, *Leptoplepis*, and *Pachycormus*. Other fossils include plants derived from nearby land, bivalves, crinoids, ammonites, belemnites, The fossils may show soft tissues, famously the body outlines of ichthyosaurs, a result of minimal decay and scavenging because of anoxic conditions (Röhl *et al.* 2001). Most of the fossils occur in black, anoxic oil shales and they are substantially compressed. Less common are specimens enclosed within the limestones, and these may be preserved in three dimensions, but they have proved hard to extract. The vertebrate faunas are similar, but Strawberry Bank has yielded much more abundant fish remains, and these and the reptiles are not flattened, as is commonly the case at Holzmaden.

Conclusion

The Strawberry Bank Lagerstätte is significant for four reasons, its contribution to our knowledge of marine life in the Early Jurassic, as evidence for unusual amounts of exceptional preservation at a time of substantial environmental perturbation, its exceptional three-dimensional preservation, and its unique insight into life in a near-coastal marine setting.

The Early Jurassic was an important time in the evolution of life, with modern-style benthic ecosystems becoming established. Among predators, decapod crustaceans, cephalopods, neopterygian fishes, and reptiles were new forms that emerged in the Triassic, during recovery from the devastating Permo-Triassic mass extinction (Benton *et al.* 2013). Many of these clades received a further setback during the end-Triassic extinction (ETE), and

they were just recovering from that crisis when the T-OAE caused further environmental stress (Friedman and Sallan 2012; Danise *et al.* 2015). The ETE had imposed a macroevolutionary bottleneck on various groups of fishes and reptiles, in which some clades, such as ichthyosaurs, bounced back in terms of diversity but not in terms of disparity (Thorne *et al.* 2011).

Fossil vertebrates and other taxa are relatively abundant in the Upper Lias of Europe, and they are especially abundant and well preserved exactly at the height of anoxia of the T-OAE (*falciferum* Zone). Likely the anoxic conditions of the time directly preserved more than the usual number of exceptional fossils at different locations in England, France, and Germany. Further, the concentration of similarly preserved entomofaunas in shallow marine sediments across Germany and England at exactly the same time, coincident with the T-OAE, is further evidence for a shared killing model, yet to be determined.

In contrast to the more famous coeval deposits of the Jet Rock and Alum Shales formations and the Posidonienschiefer, the Strawberry Bank Lagerstätte offers unusually perfect three-dimensional preservation coupled with the survival of soft tissues. Such three-dimensionality is not known from any other Early Jurassic site, except the less fossiliferous Argiles à Poissons and Couches de Belmont, and the Strawberry Bank fossils are making, and will make, significant contributions to understanding of the anatomy and palaeobiology of individual fish and reptile taxa.

Finally, the Strawberry Bank deposits were probably located closer to the coastline than coeval deposits. Evidence is the abundance of beetles (terrestrial insects) and the likelihood that the site was a nursery for marine reptiles, which are largely juveniles (Caine and Benton 2011). Further, unlike Holzmaden and Yorkshire, the succession is not dominated by black shales and it yields far fewer deep-marine fossils (e.g. ammonites, belemnites, echinoderms, brachiopods).

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Box 1. Lithology of the nodules

The Strawberry Bank fossils are preserved in buff-coloured calcareous nodules, which are at least partly depositional and certainly formed before any substantial compaction from overlying sediments or diagenesis. Though we cannot describe the exposure in the field, the lithology can be described from microfacies analysis of thin sections. The nodule matrix is a biomicritic mudstone to packstone with concentrations of sparry calcite within the voids created by macrofossils (Fig. a-d). Bioclasts consist mainly of numerous very small, mostly complete, gastropod shells (Fig. c) alongside the infrequent brachiopod, ostracod, bone and fish scale fragments. The gastropods range between 700 and 100 μm , small enough to represent a meroplanktonic larval stage, a common component of brackish-lagoonal ecosystems (Ambrogi *et al.* 1989).

There is little sorting of these bioclasts, beyond some occasional weak alignment by size along planes parallel to the nodule surface, indicating their concentric deposition (Fig. d). No definitively terrigenous clasts are evident, though mud grade terrestrial sediments may be present in low concentrations. Given the palaeogeographical, ecological, and taphonomic evidence of a nearby landmass and a warm-wet climate, fine ferruginous grains or crystals within the sediment might have been sourced from a palaeosol, such as a pedogenic laterite, but this requires further investigation.

There is some evidence for high organic content in these sediments, probably the result of anoxic conditions at the sea-sediment interface. Moore's (1866) account suggests that some of the nodules were blue-grey in the interior when originally excavated. More compelling evidence comes from a contemporary section near Charnay (Rhône-Alps Department, France), a site within the same palaeogeographic marginal sea as Strawberry Bank, which also bears nodules, with a very similar lithology, at exactly the same horizon (see *Significance*). Analysis of the sediment and nodules there shows that recent weathering

has led to preferential removal of ^{12}C -enriched organic carbon and dramatic TOC loss over most of the exposure (Suan *et al.* 2013).

[Box 1 Figure] Photomicrographs of blue-dyed, resin-impregnated thin sections of nodule matrix from Strawberry Bank. **(a)** A nodule bearing the anterior part of a partial *Pachycormus* (BRLSI M3913), the gill arches of the specimen seen in dorsoventral section to the left of the field, and the sediment is a biomicritic packstone with bioclasts including gastropods and fragments of fish bone/ scales. **(b)** Within the skull in the same section the void spaces not filled by micrite have been infilled by sparry calcite, and the main bone here is one of gill arch elements, with smaller, subtriangular structures below being transverse sections through the associated mineralized branchial rays. **(c)** The nodule matrix contains numerous minute gastropods as small as $100\mu\text{m}$ in diameter and one echinoid spine (centre, star-shaped). **(d)** Transverse section through the pectoral fin of a *Pachycormus* specimen, the matrix prepared off the dorsal surface, but the ventral surface is unprepared, and here bioclasts are less common, roughly sorted, and weakly aligned.

Box 2. The Strawberry Bank Insects

The Strawberry Bank site has yielded over 800 insect specimens, which were mentioned by Brodie (1849), but not described then or since. Moore clearly had a very good eye and collected everything, as many of the specimens are very faint, poorly preserved and fragmentary, unusual for 19th century collectors. The limestone containing the insects is slightly coarse, so the insects are often poorly preserved. They consist of wings, wing fragments, complete insects and body parts (Fig. a-e), and parts are separated from counterparts. For the rarer orders, it was straightforward to try to re-unite parts with counterparts. For the more abundant orders this was only possible where one part was

examined very soon after the other, so the totals given for the more abundant orders are probably overestimates.

Nine orders were identified among the 528 identifiable specimens. Odonata (dragonflies and damselflies) are represented by a small and a large form (19 specimens; 3.6% of identifiable specimens; Fig. c). Blattodea (cockroaches) include a small and large species, based on isolated forewings (10; 1.9%). We report here the first record of an earwig (Dermaptera) from the Upper Lias of the UK, based on a single elytron (0.2%). Orthoptera (grasshopper, crickets and locusts) are represented mainly by isolated wings (Fig. d), although some are pairs of overprinted wings, assigned to three families, some showing original striped and spotted pigmentation (35; 6.6%). Hemiptera (bugs) are abundant (47; 8.9%), consisting of complete insects and isolated wings that indicate several taxa (Fig. a, e). Most abundant are Coleoptera (beetles), represented mostly by isolated elytra, but also paired elytra and complete beetles (387; 73.7%), representing several species (Fig. b). Flies (Diptera) are very rare in the Jurassic, but we report at least a single wing here (0.2%) with wing venation consistent with *Architipula* (Limoniidae). Some incomplete wings may represent Diptera, or more likely Mecoptera (scorpionflies), close relatives (21; 4.0%). Finally, Neuroptera (lacewings) are identified from poorly preserved, incomplete wings (7; 1.3%), with at least two taxa. This compares with the five species in four families of Neuroptera reported by Whalley (1988) from the Upper Lias of Gloucestershire.

The Ilminster Upper Lias insect fauna can be compared with the Gloucestershire Alderton-Dumbleton sites (Woodward 1911; Whalley 1988), which yielded much smaller collections, and the rich German Upper Lias entomofauna, represented by over 4800 specimens, belonging to 21 orders, primarily from the localities Dobbartin, Schandelah, Grimmen, Kerkhofen, Mistelgau, and Holzmaden (Ansorge 1996, 2003). All these localities from central Europe represent similar offshore settings, and they are restricted to a narrow

temporal window coincident with the T-OAE, so providing a rich, but isolated snapshot of insect evolution during an important time before the origin of angiosperms and the evolution of insect groups associated with flowering plants. The most striking difference between the German localities and Strawberry Bank is the very high abundance of beetles in the latter, and it is uncertain whether this reflects genuine higher abundance, or some aspect of collector bias or differential preservation.

[Box 2 Figure] Insect fossils from Strawberry Bank, all from the Somerset Heritage Centre (TTNCM). (a) Spotty planthopper forewing (Hemiptera: *Fulgoridulum* sp.), TTNCM 39/2011/0594, length 6.5 mm. (b) Beetle (Coleoptera), TTNCM 39/2011/0640, length 12 mm. (c) Partial dragonfly forewing (Odonata: Liassogomphidae), TTNCM 39/2011/0509, preserved length 26 mm. (d) Grasshopper forewing (Orthoptera: Elcanidae), TTNCM 39/2011/0523, width 3.5 mm. (e) Paired bug forewings (Hemiptera: Archegocimicidae), TTNCM 39/2011/0707, width 2.7 mm.

Figure 1. (a) Geographic location of Ilminster in England. (b) Stratigraphy of the Middle and Upper Lias deposits in Somerset, England. (c) Reconstructed sedimentary log through the Lias succession at Strawberry Bank, taken from the measured section by Moore (1866, pp. 132-133). Bed numbering follows Moore (1866). His major stratigraphic subdivisions, and fossil reports (brachiopods, vertebrates) are also indicated. Abbreviations: LEPTAENA, Leptaena Beds; SFZ, Saurian and fish zone; U. CEPHALO., Upper Cephalopoda Beds. (A, B, from Pierce & Benton 2006.)

Figure 2. Fishes from Strawberry Bank. (a) Lateral view of *Pachycormus* (BRLSI M1297); note the degradation of the body to the anterior and the exposed phosphatized gut towards the ventral margin. (b) Complete specimen of *Leptolepis* (BRLSI M1259), at 10 cm long, one of the largest specimens of this genus from Strawberry Bank. (c) Anterior portion of *Pachycormus macropterus* (BRLSI M1359), prepared in ventral aspect; note the perfectly preserved branchiostegal bones and the lack of compressional distortion. (d) Detail of the ventral abdominal scales of *P. macropterus* (BRLSI M1359). (e) Detail of the pectoral fin of *P. macropterus* (BRLSI M1395).

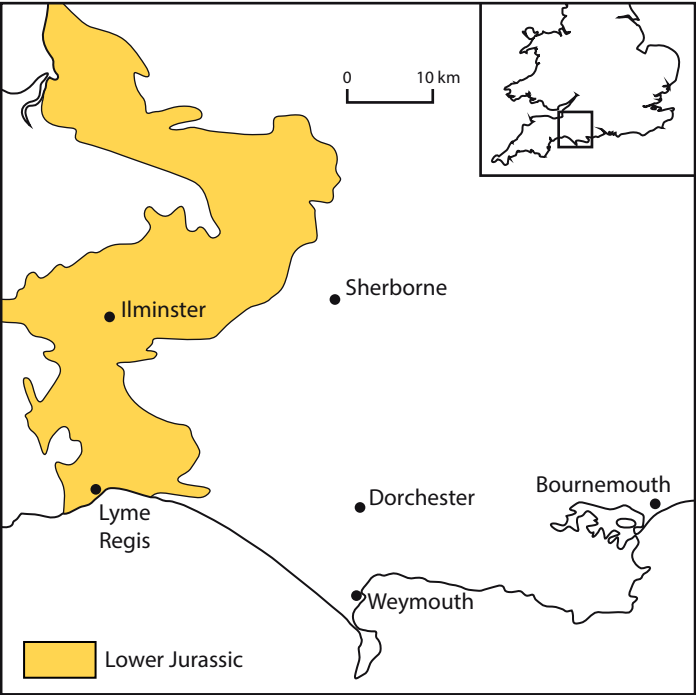
Figure 3. Reptiles from Strawberry Bank. (a, b) The skull of a juvenile ichthyosaur, *Hauffiopteryx typicus* (BRLSI M1399), in right lateral view (a), and in dorsal view, to show the lack of compression. (c) Articulated juvenile ichthyosaur, *Stenopterygius triscissus* (BRLSI M1409). (d) Skull of a sub-adult thalattosuchian crocodile *Pelagosaurus typus* (BRLSI M1413). (e) Articulated infant thalattosuchian *Pelagosaurus typus* (BRLSI M1418).

Figure 4. A reconstruction of the Strawberry Bank scene, by John Sibbick. Situated near to a sub-tropical island on the north-western margin of Tethys, the shallow seas of Strawberry

Bank provided a habitat for diverse macrofauna, amongst which early teleost fishes were the most abundant component. Here larger *Pachycormus* hunts shoaling *Leptolepis*, and opportunistically takes a mayfly that has alighted on the sea surface.

Figure 5. Soft tissues, and delicate elements, in fossils from Strawberry Bank. **(a)** Branchiostegal bones in the ventral throat region of a *Pachycormus* skull (BRLSI M1297). **(b)** Gut trace exposed beneath the disrupted scales of an articulated *Pachycormus* (BRLSI M1383). **(c)** Skin and probable muscle fibres from an ichthyosaur (genus and species unknown, as this is separation from the main specimen) (TTNCM 39/2011/0357). **(d)** Grey amorphous matter preserving the outline of the forelimb of *Hauffiopteryx typicus* (BRLSI M1399). **(e)** Soft tissue preservation of a teuthid (*Geotheuthis*?) showing preservation of the ink sac, stomach, gladius, and possibly mantle/fin structures (BRLSI M1226a).

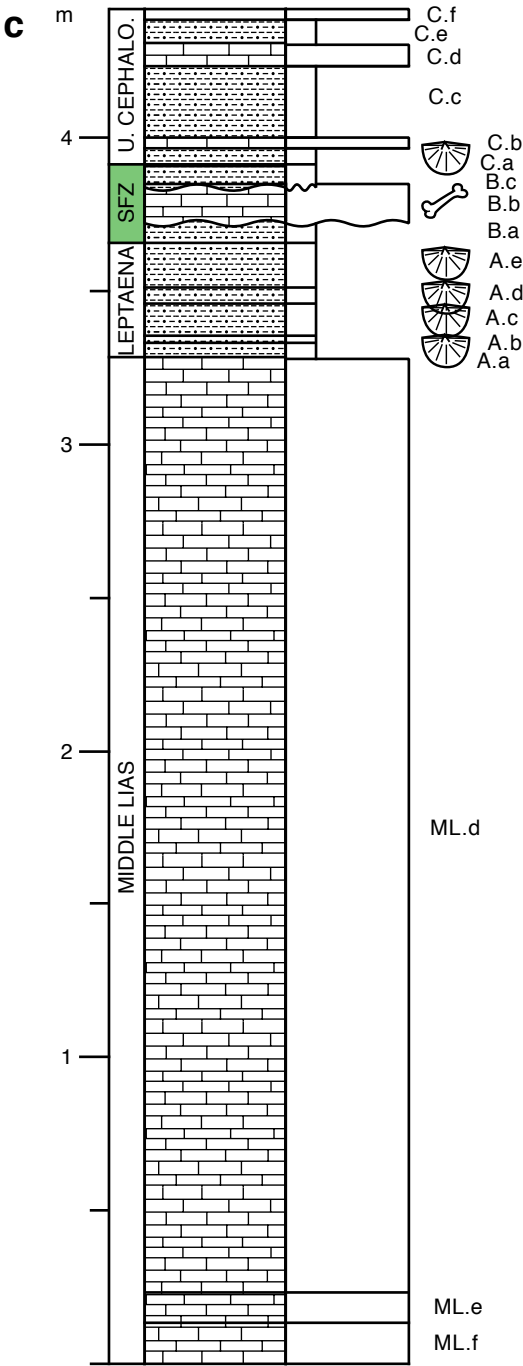
Figure 6. Comparison of key vertebrate (top row) and insect (bottom row) components of the Strawberry Bank, Holzmaden, Whitby, and Grimmer faunas. Faunal data on Holzmaden come from Hauff (1922) and other sources, and on Whitby from Benton and Taylor (1984) and other sources. Insect faunal counts come from Ansorge (2013).



a

b

Regional Classification		Ammonite Zones	Local Classification	
Toarcian (Upper Lias)	Upper	<i>thouarsense</i>	Yeovil Sands	
		<i>variabilis</i>	Cephalopod Bed	Barrington Beds
	Lower	<i>bifrons</i>		
		<i>falciferum</i>		
		<i>tenuicostatum</i>	<i>Leptaena</i> Shale	Absent (Unconformity)
Pliensbachian (Middle Lias)		<i>spinatum</i>	Marlstone	
		<i>margaritatus</i>	Pennard Sands	



a



30mm

b



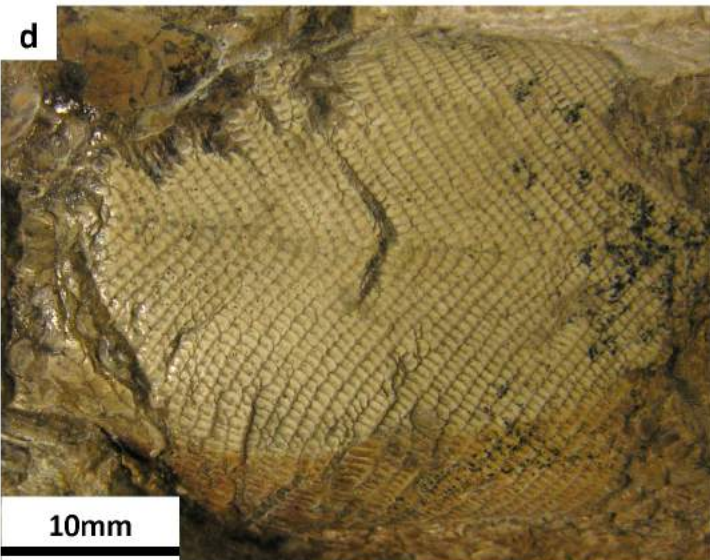
20mm

c



30mm

d



10mm

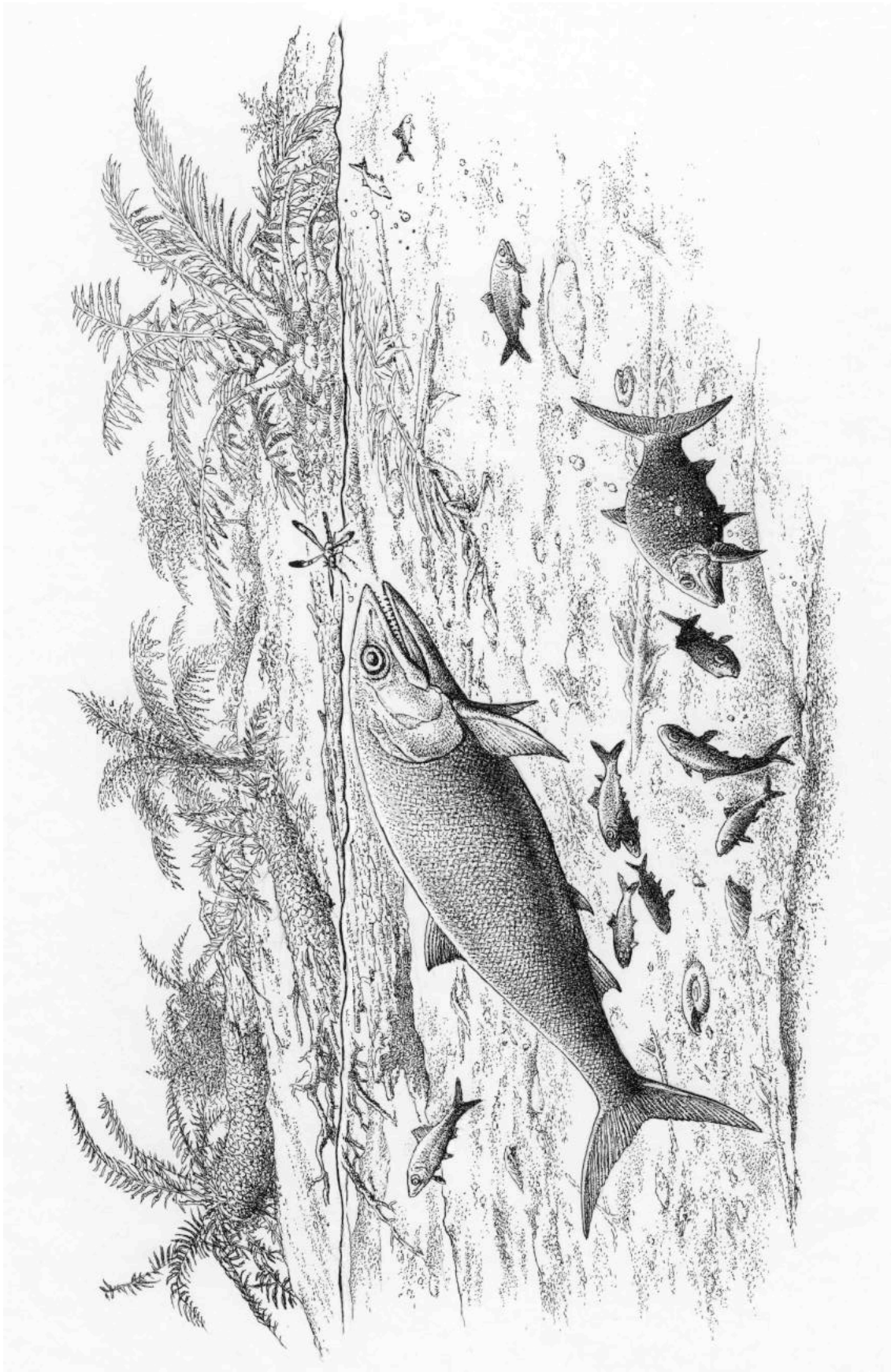
e



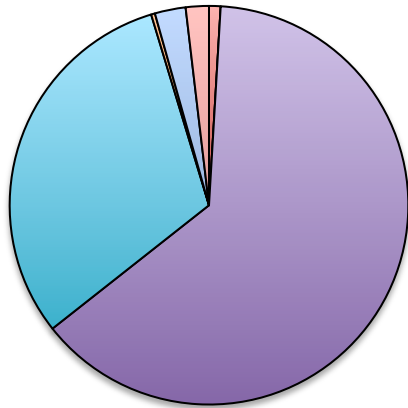
5mm



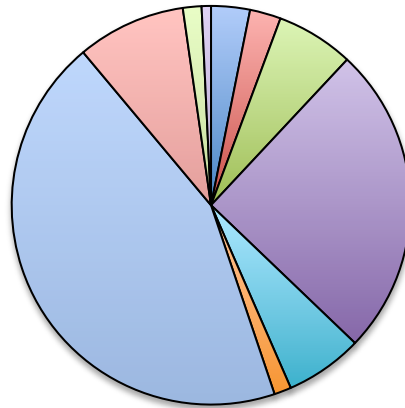




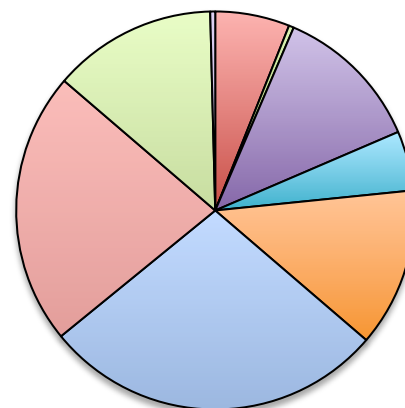
Strawberry Bank



Holzmaden

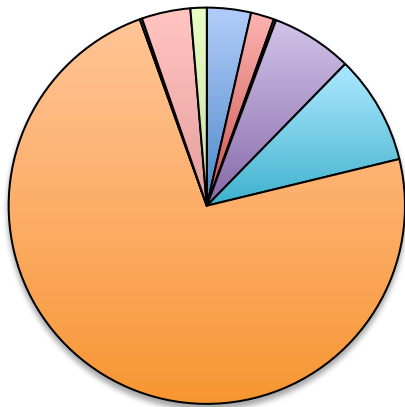


Whitby

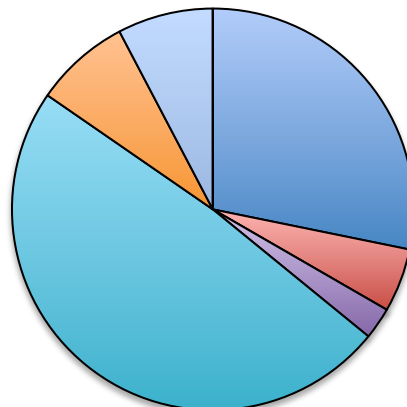


- Chondrichthyes
- *Lepidodus*
- *Dapedium*
- *Leptolepis*
- *Pachycormidae*
- Other fishes
- Ichthyosaurs
- Pelagosaurus
- *plesiosaurs*
- pterosaur

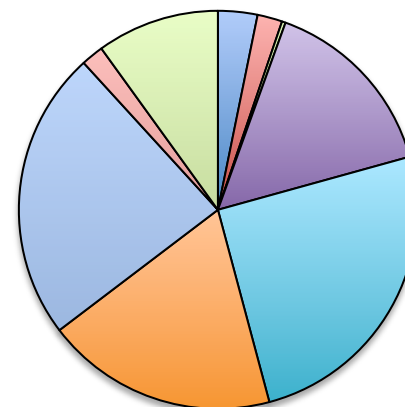
Strawberry Bank



Holzmaden



Grimmen



- Odonata
- Blattodea
- Dermaptera
- Orthoptera
- Hemiptera
- Coleoptera
- Diptera
- Mecoptera
- Neuroptera

